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Author(s): Stephen T. Emlen, Peter H. Wrege and Natalie J. Demong

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Making Decisions in the Family: An Evolutionary Perspective

The complex social interactions in a family of white-fronted bee-eaters are governed by some simple rules of reproductive success

Stephen T. Emlen, Peter H. Wrege and Natalie J. Demong

The family has been the fundamental social unit throughout much of human evolutionary history. For countless generations, most people were born, matured and died as members of extended families. However, human beings are not the only animals that form such social structures. Some of the most outstanding examples can be found among birds, of whom nearly 300 species form social bonds that are unquestionably recognizable as family units. In most cases, the family appears to play a crucial role in the socialization and survival of the individual.

The significance of the family to the development of the individual is not lost on biologists, who are inclined to ask whether certain social interactions between family members might be better understood in an evolutionary framework. Given the intensity of the interactions within a family, it is natural to expect that natural selection has shaped many of the behaviors that emerge. Could the same forces that act on birds act also on the human species? Such questions are controversial but compelling.

The evolutionary framework that is used to understand most social interaction is the theory of kin selection, for-

malized by William D. Hamilton in 1964. Hamilton emphasized that individuals can contribute genetically to future generations in two ways: directly, through the production of their own offspring, and indirectly, through their positive effects on the reproductive success of their relatives. This is because a relative's offspring also carry genes that are identical to one's own by virtue of common descent. The closer the genetic relationship, the greater the proportion of shared genes. The sum of an individual's direct and indirect contributions to the future gene pool is his or her inclusive fitness.

Because of this genetic relatedness, the social dynamics of family life is expected to differ in significant ways from the dynamics of other types of group living. The degree of kinship is predicted to influence the types of behavior exhibited among individuals. All else being equal, closely related individuals are expected to engage in fewer actions that have detrimental reproductive consequences for one another, and more actions with beneficial reproductive consequences. Although we expect significant amounts of cooperation within families, we must also recognize that not all familial interactions will be harmonious. Kinship may temper selfish behavior, but it does not eliminate it. Individuals will often differ in their degrees of relatedness to one another, in their opportunities to benefit from others, and in their abilities to wield leverage over others. These variables should predict the contexts of within-family conflicts, the identity of the participants and even the probable outcomes.

Human beings are notoriously difficult subjects for such studies because so much of our behavior is sculpted by cultural forces. In contrast, family-

dwelling birds provide excellent opportunities for testing evolutionary predictions about social interactions among relatives. They have a large repertoire of complex social behavior, yet they have few culturally transmitted behaviors that might confound the analysis. They are a natural system in which to search for fundamental biological rules of social interaction.

It is in this light that we spent eight years studying the white-fronted bee-eaters at Lake Nakuru National Park in Kenya. Our original motivation was to study the altruistic behavior of these birds, in particular their tendency to help others at the nest. We came to realize, however, that the birds simultaneously engaged in a number of selfish behaviors as well. Indeed, the birds displayed a wide range of subtle tactics, some mutually beneficial but others clearly exploitative.

An Extended Family

In biological terms, a family exists when offspring continue to interact with their parents into adulthood. This distinguishes families from temporary child-rearing associations in which young members disperse from their parents when they reach sexual maturity. We can further narrow the definition by stipulating that the parents must maintain a preferential social and sexual bond with each other. The white-fronted bee-eaters of Kenya fulfill these qualifications.

Indeed, the heart of the bee-eater society is the extended family, a multi-generational group consisting of 3 to 17 individuals. A typical family contains two or three mated pairs plus a small assortment of single birds (the unpaired and the widowed). A young bee-eater matures in a group of close relatives,

Stephen Emlen is a professor of animal behavior at Cornell University. His research focuses on cooperation and conflict in animal societies and on animal mating systems. He has also worked on the orientation, navigation and acoustic communication of birds. Peter Wrege is a research associate at Cornell where he received his Ph.D. in 1980 for his studies on the social foraging strategies of the white ibis. Natalie J. Demong is a freelance writer and photographer who specializes in avian field studies. Emlen's address: Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY 14853-2702. Internet: ste1@cornell.edu



Figure 1. White-fronted bee-eaters of Kenya provide a culture-free animal model for studying the complex dynamics within a group of closely related individuals—a family unit. Colorful tags on each member of a family allow the authors to document the interactions between specific birds. Such studies reveal that bee-eaters make sophisticated decisions based on the status and genetic relatedness of the individual with which they interact. (Photograph courtesy of Marie Read.)

and most continue to interact with parents, siblings, grandparents, uncles, aunts, nephews and nieces into adulthood. Families can even include step-relatives (stepparents and half-siblings) when individuals remate after the death or divorce of a partner. As a result, bee-eater families often have very complex genealogies.

About 15 to 25 families (100 to 200 birds) roost and nest together in a colony. The nests are excavated in sandy cliff faces where the birds dig meter-long tunnels that end in enlarged nesting chambers. Late in the afternoon all bee-eaters congregate at their colony to socialize and roost.

During pair formation, one member leaves its own family and moves to that of the other. This dispersal rule reduces the likelihood of within-family pairings; indeed, we have never witnessed an in-

cestuous pairing among bee-eaters. As a consequence, the resident member of the pair continues to live in a network of close genetic kin. As in most species of birds, it is the bee-eater females that usually disperse. A paired female becomes socially integrated into her mate's family, but the genetic kinship links are lacking. Unrelated females are the functional equivalents of "in-laws."

Once paired, bee-eaters are socially monogamous, exhibiting high mate fidelity over years. Divorce rates are low, with the effect that most individuals remain paired to the same partner for life. Both sexes share equally and heavily in all aspects of parental care.

In many respects, the social structure of bee-eaters has similarities to the supposed organization of ancestral human beings, who are thought to have formed long-term pair bonds, who lived in vil-

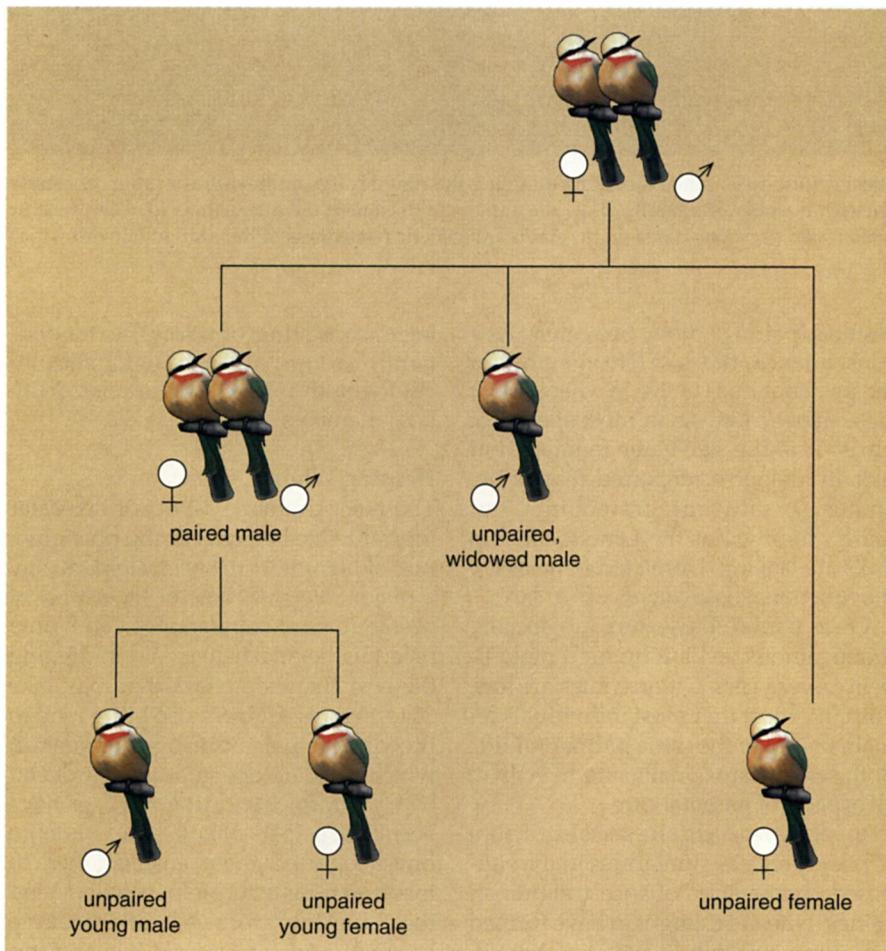
lages consisting of several extended-family groups, and whose families included both related and unrelated (in-law) members.

Helping Whom?

The most dramatic aspect of bee-eater reproductive behavior is the phenomenon of helping at the nest. Helpers play a major role in almost every aspect of nesting except copulation. Even before breeding begins, helpers aid in digging the nest chamber, a task that may take 10 to 14 days. Helpers also bring food to breeding females during the week in which they are energetically burdened by egg production. After the eggs have been laid, helpers of both sexes undergo physiological changes, enabling them to incubate the clutch. Helpers will defend the young birds for weeks after they are hatched and for several weeks after



Figure 2. Colony of white-fronted bee-eaters in the face of a sandy cliff may contain as many as 25 families, or 200 birds. The birds excavate a nesting chamber at the end of a meter-long tunnel in the wall. The colony serves as a year-round site for nesting and roosting. (Photograph courtesy of Natalie Demong.)



they are fledged. Helping usually ceases only when the young are completely self-sufficient.

By far the most significant component of helping is providing food for the young. Because the abundance of the bee-eaters' staple food (flying insects) varies unpredictably, the extraparental helpers can have a major effect on a pair's breeding success. In our study, one-half of all nestlings died of starvation before leaving the nest. However, the presence of even a single helper reduced the starvation losses to the point of doubling the fledgling success of an unaided pair!

Because bee-eaters tend to provide aid only to family members (genetic relatives), helpers play a major role in the reproductive success of their non-descendent kin. This means that helpers are indirectly increasing their own inclusive fitness. Interestingly, bee-eater helpers gain no measurable direct benefits from helping. In many other cooperative breeders (species with helpers at the nest or den) the experience of helping often translates into increased personal reproductive success later in life. This is true if the act of helping increases the likelihood that a helper will become a breeder in the future or if helping provides a better breeding slot. It is also true if the experience of helping makes one a better parent in the future. None of these personal benefits accrued to the bee-eater helpers at Nakuru; their helping behavior appears to be maintained entirely through kin selection.

If the major benefit the helpers accrue is through kin selection, bee-eaters should be sensitive to their degree of kinship to different family members. This is indeed the case. When a bee-eater faced the choice of helping one of several relatives, the helper chose to aid the most closely related breeding pair in over 90 percent of the cases (108 of 115).

Kin-selection theory also helps to explain why nearly half (44 percent) of all bee-eaters neither breed nor provide

Figure 3. Extended family of white-fronted bee-eaters may contain three or more generations of birds. Males remain in their natal family after taking a mate and are surrounded by close genetic relatives throughout most of their lives. When females pair they leave their natal group to live with their mate's family and consequently are not closely related to the birds in their new home. The difference of living with or without genetic relatives is associated with striking differences in the social interactions of paired males and females.

help in any given year. There is little profit in helping distant kin. Indeed, most nonhelpers are individuals with no close relatives in their social group. The largest subset of nonhelpers are the females who separated from their own families at the time of pairing. Helping does not increase the inclusive fitness of such females until they have raised fully grown (and breeding) offspring of their own. At this point, they again become helpers, selectively aiding their breeding sons to produce grand-offspring.

On the other hand, the benefits of helping close kin also explain instances in which birds whose own nesting attempts fail, change roles and addresses and become helpers at nests of other breeders in the family. Through such redirected helping, they can recoup much of their lost inclusive fitness. This "insurance" option is typically available only to the males, since they are more likely to be surrounded by close genetic relatives. As predicted, the vast majority (90 percent) of redirected helping involves males. Although females typically relocate to the new nesting chamber with their mate, they rarely participate in rearing unrelated young. The contrasting behaviors of the male and the female are especially striking in the light of all the stimuli—eggs, incubating adults, begging nestlings and attending adults feeding the nestlings—that

would seemingly induce the female to help at the nest.

Coercion by Parents

Since helpers have a large positive effect on nesting success, their services are a valuable resource in a bee-eater family. As a result, we would expect some competition among breeders for a helper's services, and even occasional conflicts between breeders and potential helpers over whether the latter should help. In some instances, helping at the nest might be forcefully "encouraged."

Bee-eaters do, in fact, engage in seemingly coercive behaviors that result in the disruption of nesting attempts of subordinate birds and their subsequent recruitment as helpers at the nest of the disrupter. Older birds will repeatedly interfere with the courtship feeding of a newly formed pair and block the pair from gaining access to its nesting chamber. Both actions increase the probability that the harassed pair will fail to initiate breeding and that the kin-related subordinate bird will help at the nest of the older bird.

The surprise is that the harassing birds are close genetic relatives of the pair they disrupt. Indeed, parents (mostly fathers) are the most frequent harassers; they disrupt the breeding attempts of their own sons. Over half (54 percent) of one-year-old sons whose

parents are breeding fail to breed themselves apparently because they are successfully recruited. This proportion drops as the sons become older and gain in dominance status. By the time sons are three years old, they are practically immune to coercion attempts.

The existence and the resolution of this conflict become understandable when we consider the relatively large net fitness benefit to the breeder and the small net cost to the potential helper when the latter is a son. For one thing, a son is equally related to his own offspring and his parents' offspring (which are his full siblings, provided that no cuckoldry or parasitic egg dumping has occurred). Since an unaided breeder (such as a subordinate son) produces only slightly more young on his own than he does if he contributes as a helper at another's nest, the genetic cost of the tradeoff is minimal to him. Sons apparently do not resist, because the fitness benefits of the two options are nearly equal for them. In contrast, the parents gain considerably more genetic fitness for themselves by using their son to help them increase the production of their own offspring (each of whom shares one-half of a parent's genes by descent) than they would if their son bred and produced grand-offspring (each of whom shares only one-quarter of a grandparent's genes by descent). In

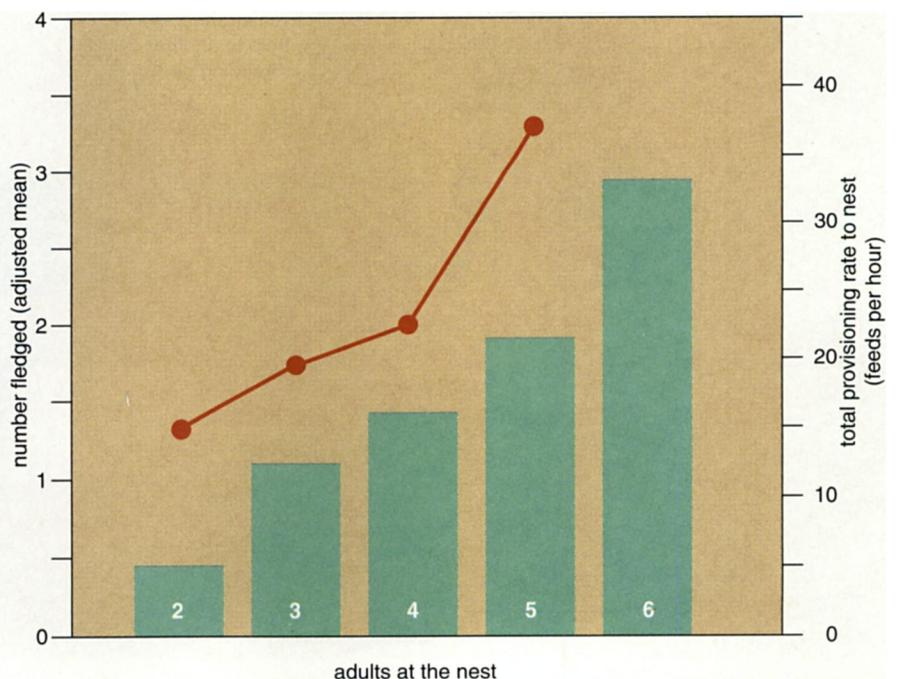


Figure 4. Feeding of juveniles by adult members of a family is crucial to the survival of the younger birds. The number of adults at the nest (right) affects the rate at which juveniles are fed (orange line), which is closely associated with the number of birds that survive to fledging status (green bars). Here adults bring food to nestlings waiting within the tunnels (left). (Photograph courtesy of Natalie Demong.)

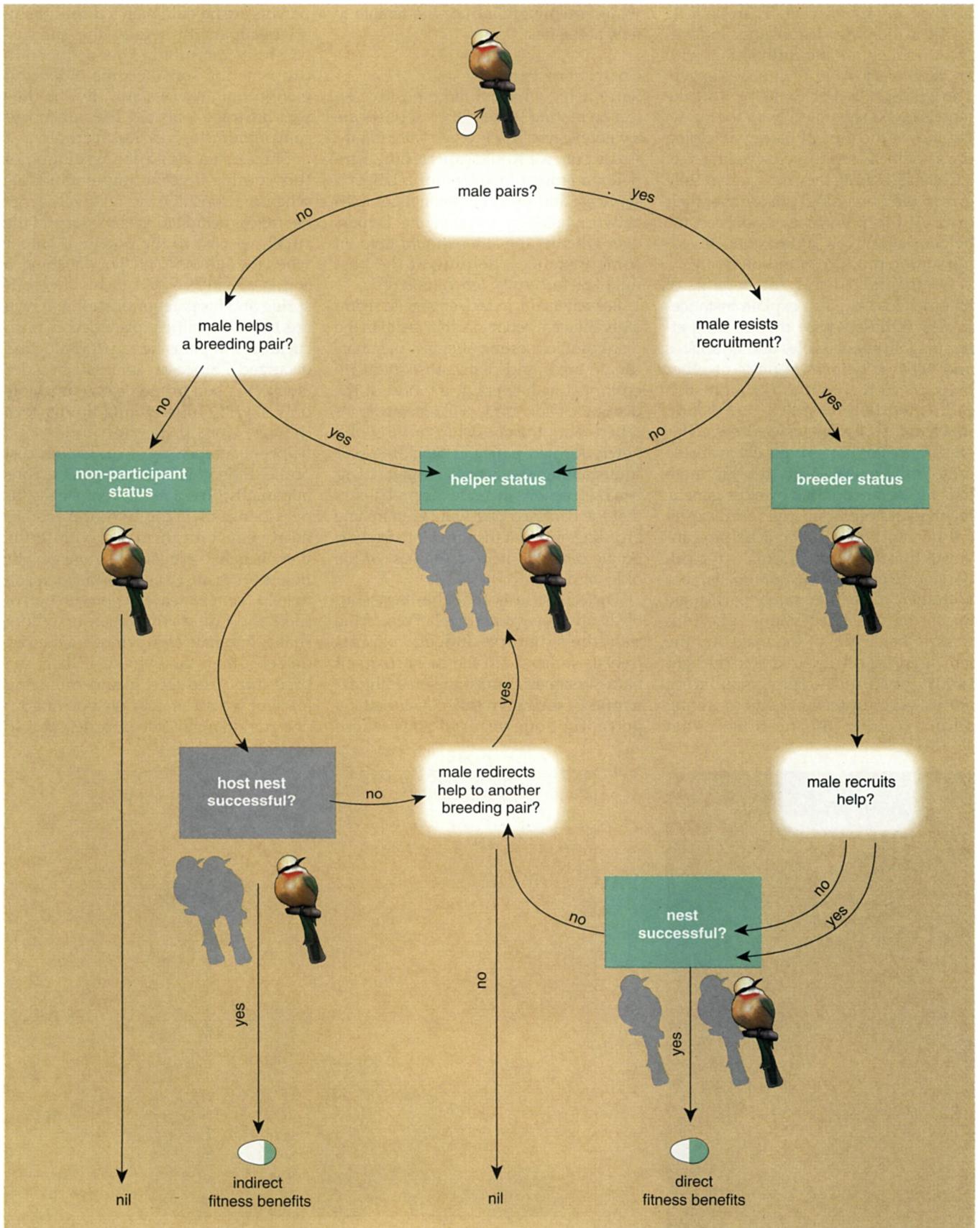


Figure 5. Male bee-eater faces a number of decisions every breeding season that influence his direct and indirect reproductive fitness. A male gets *direct* fitness benefits (corresponding to 0.5 units for each offspring produced, *green half egg*) by acquiring a mate and tending a successful nest. A male gets *indirect* fitness benefits (varying from near zero to 0.5 for each offspring produced, *green quarter egg*) by helping a close relative raise young, rather than breeding on his own. At each decision point the male generally chooses the option that maximizes his inclusive fitness.

this light, the harassment of the son by the parents makes evolutionary sense.

Other members of the family find themselves in a very different situation. Although a breeder will always gain by recruiting a helper, the cost to the helper increases dramatically when he or she is more distantly related to the harasser. Potential helpers who are distantly related to the harasser should, and do, show much greater resistance to recruitment attempts. An older dominant bird can exert leverage over a younger subordinate, but only to a point. It is not surprising then that harassers preferentially select the youngest, most closely related male family members as their targets.

The Female's Options

Since female bee-eaters break the social bonds with their natal families when they pair, their choice of reproductive options differs from those of male bee-eaters. For one thing, they largely forfeit the ability to obtain indirect benefits by helping. Unlike her mate, a female's inclusive fitness (after pairing) depends almost entirely on her success in breeding.

Since a female bee-eater lives with her mate's family, her breeding success is strongly affected by the composition and social dynamics of his family. The likelihood that the new pair will have helpers of its own, or will be able to breed unharassed by others, depends on the male's social and genealogical position within his family. We would expect females to incorporate social components of male quality in their mating choices. Females should pay attention to the prospective mate's social dominance and to the nature of his kin, who may be potential helpers or harassers.

These predictions have been confirmed. Widowed or divorced, older males with offspring of their own were nearly twice as likely to become paired as were young males with older close relatives. The older males were more likely to provide the pairing female with helpers at her initial nesting, whereas younger males were more likely to have their initial nesting disrupted.

Unpaired females who postpone the decision to take a mate retain the option of gaining indirect benefits from helping members of their natal family. Females with close breeding kin should be more likely to remain single. Again, this prediction was borne out: Females with both parents breeding were nearly twice

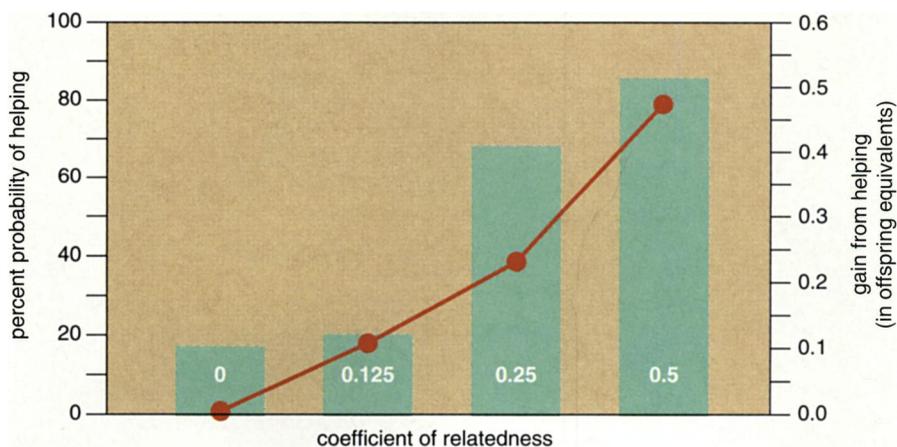


Figure 6. Helper's gain in indirect reproductive benefits (orange line) is proportional to the degree of genetic relatedness between the helper and the juvenile being helped. Not surprisingly, the degree of genetic relatedness is a strong predictor of the probability (green bars) that one bee-eater will help another.

as likely to remain single as were females with only distantly related breeders in their family.

Females appear to be making a very sophisticated assessment of their options. They act as if they compare the expected benefits of helping versus breeding. We compared the females' actual decisions to those predicted on the basis of the expected benefits given their circumstances (the identity of their breeding natal relatives and the status of their chosen mate within his family). We found that more than 90 percent of the females (67 of 74 cases) behaved as our model predicted. They paired when a potential mate was in a social position

that provided a net increase in their expected inclusive fitness benefits, but they remained in their natal families when their benefits were greater as unpaired helpers. For many females it is better to delay breeding for a season than to accept a mate of poor social standing.

After pairing, a female bee-eater is faced with another series of reproductive choices. If she succeeds in mating with a male in good standing, her problems are solved. But what options remain if her nesting attempts end in failure? Returning to her natal family to help at the nest seems to be an obvious choice, but we have seen this be-



Figure 7. Aggressive interactions take place when dominant bee-eaters attempt to recruit subordinate relatives to help raise the aggressor's offspring, rather than permit the relatives to breed on their own. Most coercive interactions take place between a father and a young son. The existence and the outcomes of such conflicts can be predicted on the basis of the reproductive benefits to the individuals. (Photograph courtesy of Natalie Demong.)

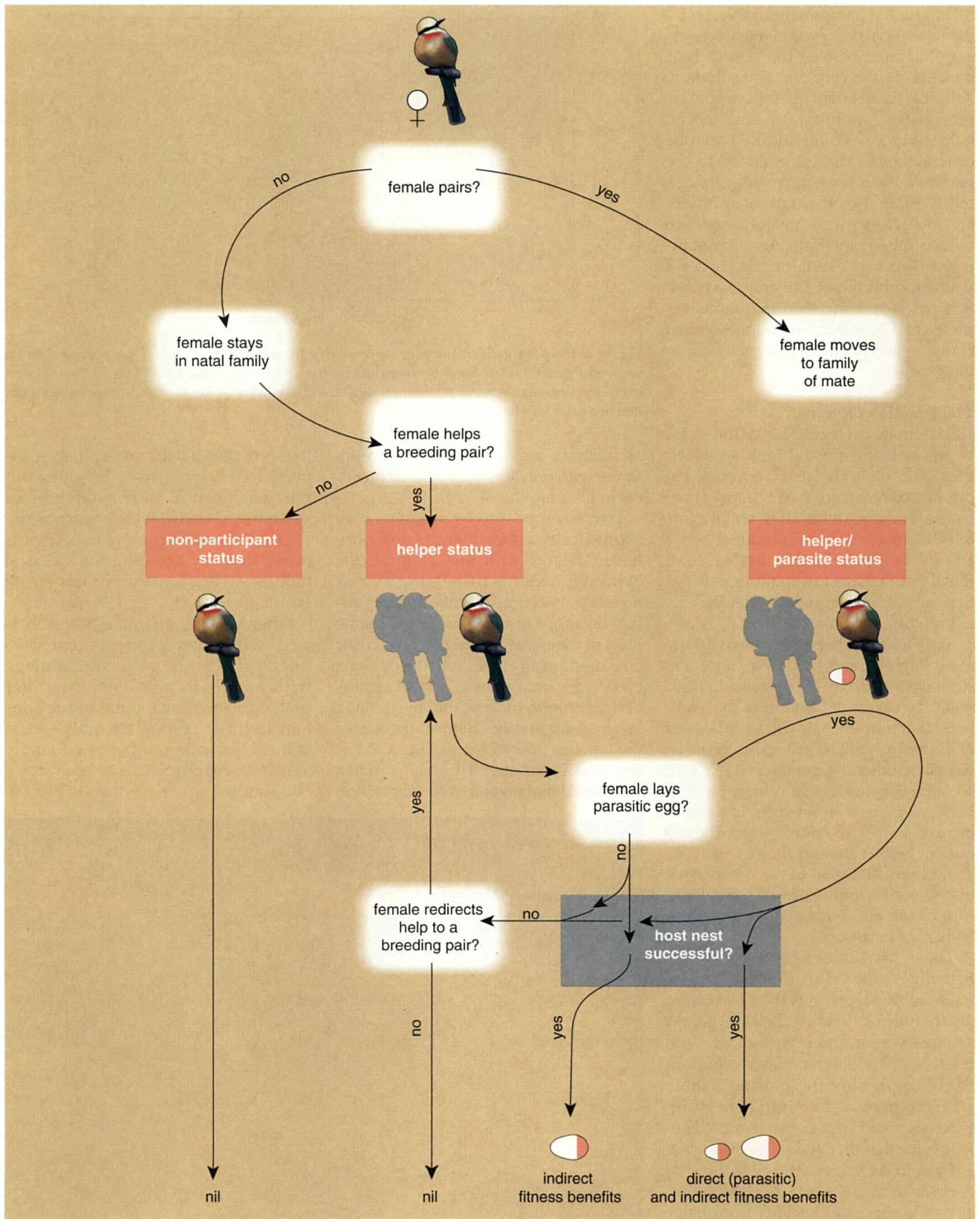


Figure 8. Female bee-eaters that choose not to mate during a breeding season stay in the natal family group. If they choose not to help during a breeding season, their net fitness benefit is nil. If they choose to help at a relative's nest, they receive *indirect* fitness benefits. Occasionally an unpaired female may copulate with a neighboring paired male and then return to the natal nest. If such a female lays a fertile egg in the nest of the relative she is helping she will receive both *direct* (small, pink half egg) and *indirect* fitness benefits (large, pink quarter egg).

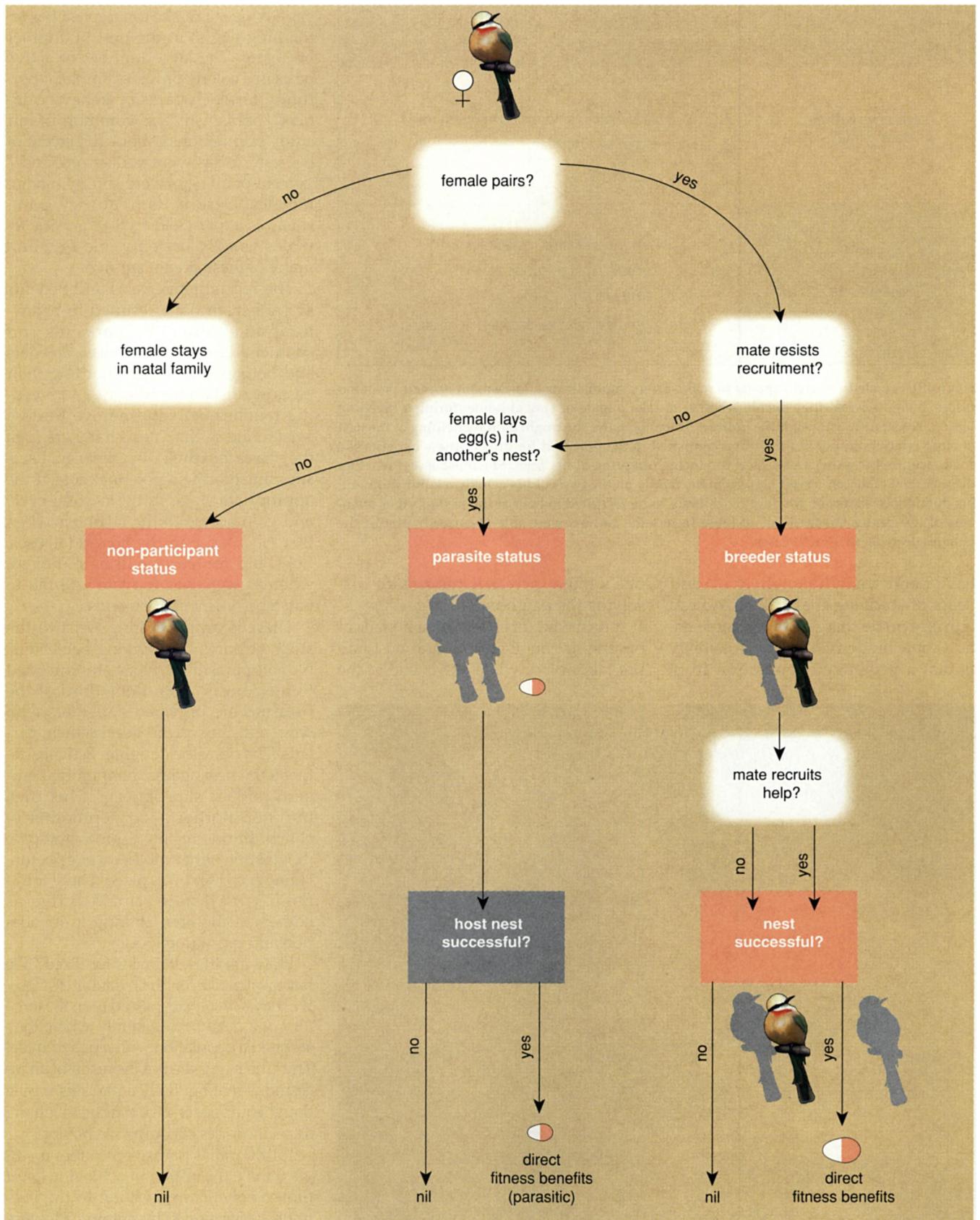


Figure 9. Female bee-eaters that take a mate leave the natal group to live with the male's family group. If the female's mate resists recruitment by his relatives, the pair can establish their own nest and receive *direct* fitness benefits (*large egg*) by having offspring. If the female's mate does not resist recruitment, a female has the option of parasitically laying her egg(s) in another's nest and still gaining direct fitness benefits (*small egg*). Parasitism is a relatively frequent tactic, with about 16 percent of nests containing a parasitic egg. If the female's mate is recruited, the female usually remains in her mate's family group but does not help raise the offspring of her mate's relatives.

factors in a female's decision whether to mate or stay in her natal group	
concerns within natal family	<ul style="list-style-type: none"> • kinship relationships to breeders • natal group size
concerns within mate's family	<ul style="list-style-type: none"> • mate's kinship relationships • mate's family group size • mate's age • mate's relative dominance position

Figure 10. Female bee-eaters appear to make a very sophisticated assessment of their potential fitness benefits when they decide whether to take a mate or stay at home during a breeding season. A female must weigh the indirect fitness benefits she might gain by helping at the nest of close relatives in her family group compared to the potential for direct fitness benefits she could acquire by taking a mate and producing offspring of her own. She must assess whether the potential mate can recruit help from his family on the basis of his genetic relationships and his dominance status, or whether he is likely to be recruited to help at the nest of other members of his family. On the basis of these factors the authors were able to correctly predict the female's decision in 67 of 74 cases.

behavior only a handful of times in eight years of studying these birds. We can only speculate that returning home entails some hidden costs. One possibility is that a prolonged separation from

one's mate increases the risk of dissolving the pair bond.

It turns out that a female who fails at nesting has another option. If nest failure takes place while she is still at the



Figure 11. Breeding female actively removes eggs laid by parasitic females before she initiates her own clutch. A successful parasite must overcome the host's defenses and lay her eggs within the two- or three-day period that the host lays her own eggs. (Photograph courtesy of Marie Read.)

egg-laying stage, she can deposit her remaining egg(s) in the nest of another bee-eater. The large number of active nests in a colony provides ample opportunity for such parasitic behavior. Indeed, parasitism was common in our study populations: About 16 percent of bee-eater nests were parasitized, and 7 percent of all eggs were laid by foreign females. Despite its frequency, parasitism is a low-yield tactic: Parasitic females usually lay only one egg, and many of these do not survive.

The reproductive costs and benefits of parasitism have resulted in behavioral adaptations by parasites and counter-adaptations by hosts. Breeders and helpers take turns guarding their nests against all trespassers, and breeding females actively remove foreign eggs found in their nest chambers until they have laid their own first egg. Parasites must locate a potential host at the appropriate stage in the nesting cycle and gain access to the chamber when there is a lapse in the host's defenses. Eggs laid too early will be removed, whereas eggs laid too late will fail to hatch before incubation ends.

There is an interesting twist to the story of parasitism among bee-eaters: Not all parasitic females are unrelated to their hosts. About one-third of the parasites are unpaired daughters who were assisting at the nest of their parents. The parasitic daughter actively defends the nest against nonfamily members, but she slips an egg of her own into her mother's (or stepmother's) clutch. In one instance, a daughter removed one of her mother's eggs before laying her own in its place. These intrafamilial parasites remain active as helpers at the nest, sharing in incubation and providing food.

How are these females fertilized? We have watched a few such daughters closely: They actively trespassed onto the territory of a neighboring family, where they solicited a copulation with a paired male! Thus their eggs are not the result of an incestuous mating. Rather, parasitism by a daughter appears to be a tactic involving a specific series of complex behaviors.

Intrafamilial parasitism offers a single female the option of achieving *direct* fitness benefits in addition to the *indirect* benefits gained by helping. However, the daughter's gain comes at the expense of the parent. It is not clear whether the parents tolerate their daughter's egg dumping to retain her as a helper or whether the daughter is

surreptitiously taking advantage of her parents. In either case, the existence of this form of parasitism underscores the flexibility of the bee-eaters' reproductive options and the subtle conflicts that take place in this species.

Conclusion

The tactics that individuals use in their interactions with one another have only recently become the subject of evolutionary analysis. This is because the expression of social tactics is very plastic: Most organisms can adopt a variety of roles according to the situation and the identity of the other participants. Early workers found it difficult to reconcile this plasticity with the view that specific genes literally determine specific behaviors. It is now recognized that natural selection can operate on the *decision-making process* itself.

As long as there is heritable variation in the decision rules that the birds use, natural selection will favor variants that result in the expression of situation-dependent behaviors that maximize the inclusive fitness of the actor. One of the pioneers of this approach, Robin Dunbar of the University College of London speaks heuristically of organisms as "fitness maximizers." They make decisions based on their ability to assess the costs and benefits of the options available to them.

We have observed that bee-eaters behave as if they assess the relative costs and benefits of pursuing different options in very complex social situations. Gender, dominance and kinship all influence the fitness tradeoffs of the various tactical alternatives available to bee-eaters. Knowing these variables allows us to predict with considerable accuracy whether an individual will attempt to breed, whether it will help at a nest and whom it will help. We can also ascertain whether a bird will be harassed and whether harassment will be successful. Differences in the behavior of genetic and nongenetic members in an extended family group would remain mysterious if it were not for the explanatory power of inclusive-fitness theory.

Gender, dominance and kinship should be important predictors of family dynamics in any species that exhibits long-term pair bonding, sex-biased dispersal and interactions where one family member can influence the reproductive success of another. Cases of breeding harassment and even reproductive suppression are common features of many species that live in family-based soci-

eties. Analyzing the fitness consequences of such behavior from the perspectives of the various participants provides an evolutionary framework for understanding such social dynamics.

Can we learn anything about the dynamics in a human family from the behavior of the bee-eaters? More than any other species, the behavior of human beings is shaped by culture. The rewards and punishments that accompany human social actions are largely determined by society. The currency human beings use in assessing the costs and benefits of a particular tactic is no longer solely based on reproductive fitness. But this does not mean that we do not possess a set of behavioral predispositions based on flexible decision rules that were adaptive in our evolutionary past. Such tendencies would have been molded during our long history of living in extended family groups. It is these underpinnings that surface more clearly in animal studies of family-dwelling species.

A small but growing number of psychologists and anthropologists are incorporating an evolutionary perspective into their studies of human families. Investigation of the roles of nonparental family members in childrearing has focused on the role of siblings (especially the mother's brother) and grandparents as human analogues of helpers at the nest. Martin Daly and Margo Wilson of McMaster University have studied the effects of relatedness (parent versus stepparent) on child abuse. Robert Trivers, now of Rutgers University, has looked at the theoretical basis for parent-offspring conflict. Trivers and his colleague Dan Willard have proposed an evolutionary hypothesis to explain why some parents invest unequally in their sons and daughters.

We believe that an evolutionary framework has great potential for increasing our understanding of the social dynamics of family-based societies. By focusing on the fitness consequences of different actions to different individuals, it provides a functional explanation for why particular behavioral predispositions may have evolved. It also provides a theoretical basis for predicting the social roles that different individuals will adopt under differing circumstances. We fully expect that the same general variables found to be important predictors of bee-eater behavior—gender, dominance and kinship—will be important predictors of cooperation, conflict and

the resolution of conflict, in most other social species, including human beings. We expect that the incorporation of this Darwinian approach into the social sciences will provide a valuable additional perspective to our understanding of human family interactions.

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